# Stable oxygen isotopes reveal cooling events during the early Pliocene in the southern North Sea Basin: a multi-species approach.

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## Abstract

Oxygen stable isotope ($\delta^{18}O$) analysis of marine biogenic carbonates is widely used to study the temperature at which the hard parts precipitated. This technique enables investigation of the environmental conditions experienced by carbonate-shelled organisms throughout their life. We used this approach on four bivalve species from the Coralline Crag Formation (Early Pliocene; United Kingdom), where warm- and cold-associated species co-occur in the Ramsholt Member. Our results reveal species-specific differences in reconstructed temperature. Two distinct climatic settings were identified: a cold setting with seafloor temperatures below 7 °C in winter and 10 °C in summer, and a warm one with seafloor temperatures ranging from 8–10 °C in winter to above 15 °C in summer. These absolute temperatures were calculated using a modelled value of seawater $\delta^{18}O$ (+0.1 ‰) that is open to question, but the disparity in temperatures exists whatever value is used. Interestingly, the reconstructed temperatures for some of the studied species align with those of their modern relatives: *Arctica islandica* records the coldest temperatures in this dataset, while *Centrocardita squamulosa ampla* indicates warmer conditions. *Aequipecten opercularis*, a eurythermal pectinid, exhibited the broadest range of temperatures. The interval during which the Coralline Crag was deposited (c. 4.4–3.8 Ma) is generally regarded as relatively warm. However, the presence of *A. islandica* and the absolute seawater temperatures derived from shell $\delta^{18}O$ suggest the occurrence of sufficiently long cool periods for the establishment and survival of this long-lived species. Data from specimens of *C. squamulosa ampla* and *A. islandica* collected from a single bed point to glacial/interglacial-type climate fluctuation. These results confirm that the presence of *A. islandica* is a marker for cold temperate environments. These results also confirm that assemblage information is not sufficient to determine palaeoclimatic conditions, and that reconstructed temperatures from shell $\delta^{18}O$ can reveal time-averaging in fossil shell beds.

## Introduction

The Pliocene epoch is generally considered as warm, with global mean surface temperature (GMST) 2–3 $^{0}$C above pre-industrial levels during the Mid-Piacenzian Warm Period (Dowsett *et al*., 2013), making this interval an analogue for the end of the 21$^{st}$ century. GMST was also generally higher than now in the Early Pliocene (Fedorov *et al.*, 2013) but then, as at other times, regional climate may not have followed the global pattern. In the United Kingdom, the Early Pliocene is represented by the Coralline Crag Formation, in Suffolk, which offers an opportunity to track the climate of this period in the southern North Sea Basin.

The Coralline Crag Formation is a 15–20 m thick marine deposit, extending 15 km in a south-west/north-east direction in the Orford/Aldeburgh area of Suffolk, eastern England, where it unconformably overlies the Palaeocene–Eocene London Clay (Fig. 1; Balson *et al.*, 1993). Based on the distribution of dinoflagellates, the Coralline Crag has been attributed to the mid–late Zanclean stage (Early Pliocene), between 4.4 and 3.8 Ma (Andrew & West, 1977; De Schepper *et al*., 2009). The Coralline Crag is the only onshore marine formation of Early Pliocene age within the United Kingdom, providing valuable insights into the marine environment of the North Atlantic region. Due to the richness of its fauna, this formation has drawn the attention of palaeontologists and taxonomists since the 19$^{th}$ century (Charlesworth, 1835; Wood,1848; Prestwich, 1871) and continues to do so: the good preservation of malacofauna specimens has led to several recent geochemical works (Johnson *et al.*, 2009, 2021; Vignols *et al.*, 2019). The Coralline Crag is composed of three members, the Ramsholt Member, Sudbourne Member and Aldeburgh Member (Fig. 1). According to Balson *et al.* (1993), the Ramsholt Member has low mud content (< 7%) and low $CaCO_3$ content (35 – 50%). Both calcitic and aragonitic shells are well preserved, the latter being predominant (up to 64%). Silty sands and extensive bioturbation suggest relatively slow bottom currents and a low sedimentation rate. The overlying Sudbourne Member shows higher $CaCO_3$ content (65% on average), but due to post-depositional dissolution, aragonite is generally absent. The Sudbourne Member is considered to have been deposited in a relatively high-energy environment, as suggested by the presence of large-scale cross-stratification, the scarcity of *in-situ* fauna and the abrasion of most of the skeletal debris. The Aldeburgh Member (probably a lateral equivalent of the Sudbourne Member) is similar to the upper Ramsholt Member and the Sudbourne Member in terms of mud and $CaCO_3$ content, and like the Sudbourne Member, aragonite is mostly absent.

One of the most striking features of the Coralline Crag is the diversity of its malacofauna: Prestwich (1871) recorded 316 different mollusc species, 185 still occurring today around the British Isles. Long & Zalasiewicz (2011) reported 219 mollusc species in samples from one locality, Raydon Hall. Both studies acknowledge the fact that species with different biogeographical character co-occur, especially in the Ramsholt Member. Based on the assumption that the thermal niche of a species remains stable through time (ecological uniformitarianism), a boreal and a Lusitanian component has been described. The cold-associated bivalves include *Mya truncata* (Linnaeus 1758), *Macoma obliqua* (J. Sowerby 1817), *Cyrtodaria angusta* (Nyst & Westendorp, 1839), *Pygocardia rustica* (J. Sowerby 1818) and the long-lived *Arctica islandica* (Linnaeus 1767)(Long & Zalasiewicz, 2011). The 'warm' bivalve taxa include *Centrocardita squamulosa ampla* (Chavan & Coatman 1943) and *Panopea glycymeris* (Born 1778) (Long & Zalasiewicz, 2011). Furthermore, thermophilous bryozoans (*Cupuladria, Metrarabdotos*) occur abundantly in the Ramsholt Member: today they occur off west Africa and in the Caribbean (Lagaiij, 1963; Cheetham, 1967, Balson, 1983). Also thermophilous ostracod species (Williams *et al.*, 2009; Wood *et al.*, 1993) and dinoflagellates (Head, 1997) are reported. The climatic conditions under which the Coralline Crag was deposited are still unclear. The bivalve taxa generally represent a fully marine, open shelf setting, with a well-developed thermocline and low tidal currents during deposition of the Ramsholt Member (Daley & Balson, 1999). The depth of deposition of the sediments of this Member remains difficult to determine, but previously cited authors agree that 50 m is the most realistic estimate (Johnson *et al.*, 2009). To produce a more precise paleoenvironmental reconstruction, the first step is to get more detailed information on the depositional processes and try to determine if some taxa are limited to specific horizons in the Ramsholt Member. A post-depositional reworking of shell material could have caused mixing of species that lived at different times (and thus in different climatic conditions) or in different environments. Stable oxygen isotope ($\delta^{18}O$) analysis will allow us to determine if shell specimens lived under similar thermal environments. With these approaches we aimed to answer the following questions about the Coralline Crag deposition and its climatic conditions:

- Is it possible to determine if boreal and Lusitanian faunas of the Coralline Crag lived contemporaneously?
- If so, did they live in the same environment?
- If not, which depositional conditions led to this specific assemblage?

## Material and methods

*Excavation of the Sudbourne Park exposure*

This study is focused on the Ramsholt Member of the Sudbourne Park locality near Orford (Suffolk) to constrain the complexity of the paleo-environmental reconstructions and to limit the diversity of faunas represented in specific horizons of the Ramsholt Member. An excavation conducted in June 2023 with the permission of Natural England (the locality is a designated Site of Special Scientific Interest) allowed precise description of the section and collection of well-preserved, sometime articulated specimens of different species of interest, and documentation of their respective positions in the section.

*Taxa and specimen selection*

Four different bivalve species present in the Coralline Crag were selected for geochemical analysis for seawater temperature determination: *Aequipecten opercularis* (Linnaeus 1758); *Arctica islandica* (Linnaeus 1767); *Glycymeris obovata* (Lamarck 1819); and *Centrocardita squamulosa ampla* (Chavan & Coatman 1943). The latter taxon is sometimes named *Cardites squamulosa ampla* (e.g., Lauriat-Rage, 1981; Wesselingh & Moerdijk, 2010) but its closest living relative is *Centrocardita aculeata* (Poli 1795) (type species of *Centrocardita*, which is distinguished by the presence of a small anterior lateral tooth and an anterior 3a cardinal tooth on the right valve; Glibert & van de Poel, 1970 and own observations).

*A. opercularis* is considered as eurythermal and fast-growing (Johnson *et al.*, 2009) and used as a control. *A. islandica* and *G. obovata* are long-living species representing the boreal fauna (according to Vignols *et al*. 2019), and *C. squamulosa ampla* represents the Lusitanian group. A total of 16 shells were analysed, nine collected directly by the authors and seven kindly provided by Ipswich Museum and the Sedgwick Museum (University of Cambridge). When possible, and to avoid reworked material, articulated shells were used. The details of the 16 specimens can be found in Table 1.

*Shell integrity assessment of the selected specimens: SEM analysis*

As post-depositional alteration of the shell structure can alter the isotope signal (especially in aragonitic shells), it is essential to check the integrity of the shell material before geochemical

analysis, even if specimens look excellently preserved (Balson, 1983). The carbonate shells of bivalves are produced under biologically controlled conditions, and therefore show specific ultrastructures (Marin, 2012). Visual inspection of these ultrastructures under Scanning Electron Microscope allows us to determine if the structure is altered or show signs of recrystallisation. Selected shells were encased in Buehler Epothin-2 resin, cut along the major growth axis, and polished for better visibility of the internal growth features of the shells. Cross-sections of aragonitic shells (*A. islandica*, *C. squamulosa ampla* and *G. obovata*) were etched in a 1vol% HCl solution, coated in gold, and observed at the Scanning Electron Microscope Facility of the University of Derby. *A. opercularis* preservation was checked according to the method used in Johnson *et al.* (2009).

*Stable isotope analysis*

Carbonate sample collection was performed with a vice-mounted hand-drill equipped with a 300 µm diameter conical SiC drill bit, on cross-sections (inner portion of the outer shell layer) for aragonitic shells and on the outer shell surface (outer portion of outer shell layer) for the calcitic *Aequipecten* shells. For both type of shells, samples were sequentially collected along the maximum growth axis, from the hinge toward the ventral margin, with a distance between each drill spot of 50 to 350µm. The sample height (distance between each drill spot and the origin of growth) was measured through ImageJ. Significant growth lines were noted and associated with their isotopic samples to detect any growth break in the produced $\delta^{18}O$ profiles. 80–150 µg carbonate powder samples were analysed at the University of Mainz (Germany) with a ThermoFisher MAT 253 mass spectrometer coupled with a Gasbench II or at the British Geological Survey facility (Keyworth, UK) with an Isoprime dual inlet mass spectrometer coupled with a Multiprep system. Isotopic data were calibrated with NBS-19 and Carrara marble standard against Vienna Pee Dee Belemnite (VPDB).

*Temperature reconstruction from $\delta^{18}O$*

As both calcitic and aragonitic shells were analysed, two different equations were used, depending on the considered species. Aragonitic $\delta^{18}O$ values were transformed to temperatures according to the equation established by Grossman & Ku (1986) with a VSMOW–VPDB scale correction of –0.27 ‰ (see Dettman *et al.*, 1999):

$$(1)\quad T\ (°C) = 20.60 - 4.34\ (\delta^{18}O_{aragonite} - (\delta^{18}O_{sw} - 0.27)),$$

where $\delta^{18}O_{sw}$ is the oxygen isotopic composition of seawater. The calcitic $\delta^{18}O$ values were converted to temperatures using the O'Neil *et al.*(1969) equation, following previous work on Coralline Crag *A. opercularis* shells (Johnson *et al.*, 2009; Vignols et al. 2019) :

$$(2)\ T\ (°C) = 16.90 - 4.38\ (\delta^{18}O_{calcite} - \delta^{18}O_{sw}) + 0.10\ ((\delta^{18}O_{calcite} - \delta^{18}O_{sw})^2$$

The VSMOW–VPDB correction was achieved by subtracting 0.27 ‰ from the $\delta^{18}O_{sw}$ value. A $\delta^{18}O_{sw}$ value of +0.10‰ was used, in the middle of the range of global average estimates and site-specific modelled values for $\delta^{18}O_{sw}$ (Buchardt & Símonarson, 2003; Johnson *et al.*, 2009).

# Results

*The Sudbourne Park outcrop sequence*

The stratigraphy of the Sudbourne Park excavation site is described in Figure 2. The section consists mainly of grey-yellow bioclastic arenites. It is divided into two units: the lower Unit II is bioturbated and dominated by small shells and shell fragments, with excellent preservation and little induration. The upper Unit I contains more sorted and worn shell fragments and represents a transgressive, possibly shallowing, higher-energy environment with the appearance of physical sedimentary structures (hummocky cross-stratification and possibly low-angle crossbedding). Contrary to Daley & Balson (1999), we suggest that the upper unit belongs to the Sudbourne Member and not the Ramsholt Member, although we retain the assignment to the latter for present purposes. For more details, see Figure 2 and Supplementary material 1). Four distinct shell beds (SB) were described: SBI at 115 cm (Unit I), SBII at 170 cm (Unit I), SBIII at 280 cm (Unit II) and SBIV at 330 cm (Unit II) depth below surface.

SBII was particularly investigated, as the four species of interest are well-represented. In terms of relative abundance in this bed, *C. squamulosa ampla* was dominant, and *A. islandica* and *G. obovata* were common, with some *A. opercularis*. Most of the shells showed no preferential orientation and looked well-preserved, with most being complete and little abraded. Considering the fragility of the outer layer of both modern and fossil *Centrocardita* shells, we conclude that "the Shell Beds do not result from reworking of material from elsewhere or from lower levels in the sequence but from essentially in situ accumulation under circumstances of low sedimentation" (Supplementary material 2). The only paired specimen of *C. squamulosa ampla* also comes from this shell bed. The close vicinity of the different species within SBII is illustrated by Figure 3.

*Preservation state of aragonitic and calcitic shells*

Scanning electron microscopy of the three aragonitic species confirms pristine preservation of the ultrastructures of the shells. *C. squamulosa ampla* specimens contain well-preserved crossed-lamellar ultrastructure in the inner portion of the outer shell layer (iOSL, see Fig. 4A), the specific shell layer in which the carbonate samples were collected. The *A. islandica* specimens also showed typical crossed-acicular ultrastructure in the iOSL (Fig. 4B). Aragonitic crossed-lamellar ultrastructure of the iOSL of *G. obovata* was well-preserved too, and the

hollow tubules showed no cement infill (Fig. 4C). Finally, *A. opercularis* images do not show any sign of recrystallisation of the calcite foliae (Fig 4D).

*Carbon and oxygen isotopic profiles*

Carbon and oxygen isotopic profiles are shown in Figures 5–8 (left column; raw data in Supplementary material 2). Major and minor growth lines were noted during the drilling of the carbonate samples, and they are represented by vertical solid and dotted black lines, respectively, on figures. Despite unequal growth rates resulting in unequal numbers of years recorded for each shell, all the specimens show cyclical variations of $\delta^{18}O$, except *A. islandica* specimens UD53431 and UD53432 (Fig. 5A, C). Coupled with the good preservation of the ultrastructure assessed through SEM observations, these variations can be read as seasonal records of sea-surface temperature (under the assumption of stable salinity and hence $\delta^{18}O_{sw}$). The isotopic values from UD53431 and UD53432 are within the range of other *A. islandica* specimens, suggesting that their profiles represent incomplete seasonal records. A summary of the $\delta^{18}O$ values and associated palaeotemperatures can be found in Table 2. These results will be discussed later in terms of maximal seasonal range (difference between the maximal and minimal values) for a single specimen or a taxon; and in terms of seasonal average (all the seasonal maxima or minima averaged together) for a specimen or a taxon. Boxplots of data from the four shells from SBII are displayed in Figure 9. Isotopic values from this horizon do not significantly differ from the rest of the data set (Wilcoxon's test, p-value = 0.139).

*Arctica islandica*

The $\delta^{18}O$ values of *A. islandica* shells are on average the highest in the dataset, corresponding to relatively cold temperatures in summer and in winter (see Table 2). The maximum seasonal range (as the difference between the highest winter and lowest summer, among all specimens and all years) is 1.70 ‰, while the typical seasonal range for a single year is about 0.6 ‰. The number of recorded years ranges from less than one (UD53532 and UD 53433) to six (UD53434). Carbon isotope values are in phase with $\delta^{18}O$ only for the shell UD 53432. Specimen UD53434 shows no $\delta^{18}O/\delta^{13}C$ correlation along the entire shell profile. Specimens UD51431 and UD53433 have carbon and oxygen ratios in antiphase, and specimen

IPSMG:EF.2022.23333 shows a mix between constant $\delta^{13}C$ (slightly above +2.5 ‰) in the first 12 samples of the profile, and then an antiphase correlation.

*Aequipecten opercularis*

The $\delta^{18}O$ values of *A. opercularis* shells show the widest range of the data set, with a difference of 3.01 ‰ between the extreme values, while the typical seasonal range for a single year is about 1.6 ‰. This corresponds to much more pronounced seasonal temperature variation compared to the other species. The number of recorded years varies from ≈ 1 (C36478) to ≈ 3.5 (C36472). The shell C36478 shows a remarkably well-resolved winter, spanning over 1.5 cm of growth, with no signs of growth interruption, and $\delta^{18}O$ values around +1.0 ‰. Interestingly, this specimen also has the lowest $\delta^{18}O$ value of –0.93 ‰, which corresponds to the warmest temperature of this data set (see below). $\delta^{13}C$ and $\delta^{18}O$ values are in phase for shells UD53431 and C36478 but show no correlation for specimen C36472.

*Centrocardita squamulosa ampla* and *Glycymeris obovata*

The $\delta^{18}O$ values of *C. squamulosa ampla* and *G. obovata* are very similar, both in winter and in summer (see Table 2), with median values of +1.82 ‰ and +1.77‰ respectively, and the maximum ranges are +1.68 ‰ and +1.69 ‰ respectively. The typical seasonal range is 0.4 ‰ for *C. squamulosa ampla* and +0.7 ‰ for *Glycymeris obovata*. The number of recorded years goes from 3 (UD 53412; UD53430) to 5 (UD 53429) and 6 (C3656).

*Temperature reconstruction*

Reconstructed temperature profiles for each shell are shown in Figures 5–8 (right column). The coldest reconstructed temperatures are from *A. islandica*, with winter around 6–7 $^0$C and summer at 12 $^0$C. Both *C. squamulosa ampla* and *G. obovata* show similar warmer conditions, with 10–12 $^0$C in winter and 14–15 $^0$C in summer. *A. opercularis* has the widest temperature range, with winter temperatures close to 7–8 $^0$C and summer temperatures slightly above 15 $^0$C on average and peaking at 20.3 $^0$C for the shell C36478 (see Table 2).

## Discussion

*The growth problem: do differences in thermal tolerances and phenology lead to differential records of the same environment?*

Just like the faunal composition, our isotopic results show contrasting temperature regimes, which could not be linked with specific horizons in the field. Different hypotheses can be formulated to explain this, which will be discussed below.

Mollusc growth is modulated by several environmental and physiological factors, and the isotopic profile obtained through sequential carbonate collection may not fully reflect the conditions experienced by the animal in its environment. Seasonal variation in growth rates and growth halts need to be taken in account during the interpretation of stable isotope profiles (Goodwin, *et al*., 2003). For fully marine species, living in open shelf settings with little salinity change, the main drivers of these growth variations are temperature and reproduction, when energy is allocated to gamete production instead of growth (Schöne *et al*., 2005; Royer *et al*., 2013; Ballesta-Artero *et al*., 2018;). As these growth retardations and eventually cessations are likely to occur when temperature reaches thermal tolerances of species or during the reproduction period, some part of the seasonal cycle can be missed in the isotopic reconstruction. This is particularly true for slow-growing species and typically observed in adult stages (toward the ventral margin), where growth rates drop, and the profile resolution is reduced as a result.

In modern *A. islandica* shells, growth slowdown typically occurs a month or so after the seasonal temperature maximum and lasts for about two or three months, e.g., in shallow settings in the North Sea, from September to November (Schöne *et al.*, 2005). This implies a reproductive control. In our results, growth lines also correspond to a period of decreasing sea surface temperature (SST), at least for three specimens (UD 53434; IPSMG:EF.2022.2333.3 and UD53434). These results suggest a similar timing of reproduction in the Pliocene and today. The lack of major growth lines during annual thermal minima and maxima implies that temperature reconstructions for this species capture summer and winter conditions well. The three analysed specimens of *A. opercularis* do not show a major growth line during their first year, suggesting that they contain a complete seasonal record of the temperature conditions, especially since this species is growing relatively fast, resulting in high-resolution isotopic profiles.

*C. squamulosa ampla* specimens show only minor growth lines, usually occurring in the summer–early autumn range, suggesting either a growth reduction caused by thermal stress during the warmest month, or a gonad maturation and spawning during this period. Finally, *G. obovata* growth line formation is more difficult to interpret, as lines occur at different times of the year, with no clear pattern (Figure 5). Nonetheless, some annual cycles are recorded without a major growth line during winter and/or summer extremes, allowing us to recognise several complete seasonal cycles for this species.

The slow growth rates of some shells result in low-resolution temperature profiles, which might fail to reflect the complete thermal cycle. *A. islandica* profiles contain nine (UD53434) to 15 (UD53433) samples per year, while *A. opercularis,* the fastest growing species in the data set, provided 24 samples for a single year (shell C36478). The two other species are once again similar, providing on average 6–7 samples per year. These differences in resolution of the profiles could induce bias in the record of seasonal range but this is compensated by the fact that slow-growing taxa typically have more years per profile (see Table 3): *Aequipecten opercularis* might be the species with the fastest growth of our data set, but it is also the taxon for which we have the lowest numbers of the same seasons (winters and summers) recorded. The average number of samples per season (total number of samples divided by the combined total of summers and winters) is thus similar for *A. opercularis* and *A. islandica* (6.8 and 6.7 respectively). Once again, *G. obovata* and *C. squamulosa ampla* are also close: 3.9 and 3.5 samples per season, respectively. The fact that the major growth lines do not usually occur during the annual minima and maxima also support the strength of the interspecific comparison; moreover, none of the species have blatantly truncated profiles. We thus suggest that the differences in terms of reconstructed temperature (Fig. 10) can be interpreted as differences in environmental conditions rather than differences in the period of growth.

Today, *A. islandica* is a boreal species (Ridgway *et al*., 2012). There are scanty records from the Bay of Biscay and the Iberian Peninsula, but these are based on shells from deposits of the last glaciation (Urra *et al.*, 2023), and the species nowadays has its southern limit around 48°N and does not enter the Bay of Biscay (Glémarec, 1978). *C. squamulosa ampla* is extinct, so its physiological preferences will remain uncertain. However, the closest extant relative of this species, *Centrocardita aculeata,* lives in the Mediterranean Sea and, in the Atlantic, from southern Portugal southwards to Senegal (von Cosel & Gofas, 2019), suggesting that *C. squamulosa ampla* might have Lusitanian affinities. Off the southern Iberian Peninsula, *C. aculeata* is found on outer shelf bioclastic bottoms where bottom sea-water temperatures vary

little around 14°C year-round (Puig *et al*., 2004). *G. obovata* is extinct too, but its modern relative, *G. glycymeris* (Linnaeus 1758) can be found from Norway (Lande, 1975) to the Mediterranean Sea (Purroy *et al.*, 2016) but has only scanty records from the Southern North Sea basin (Seaward, 1990). *A. opercularis* is a eurythermal species and its modern distribution in the North Sea (Seawards, 1990) overlaps the distribution of modern *A. islandica*. One might argue that if these different species had different thermal affinities, they would show maximum annual growth at different seasons, e.g. *A. islandica* predominantly reflecting winter conditions and *C. squamulosa ampla* and *G. obovata* predominantly reflecting summer conditions. This is known to be the case for modern *G. glycymeris* of Scotland, whose isotopic signatures mainly represent spring and summer temperatures (Reynolds *et al.*, 2017). This would however be counterbalanced by the use of a fast-growing pectinid like *A. opercularis* that can help provide complete, year-long high-resolution profiles of temperature (Hickson *et al*., 2000). Thus, this method can help to detect the eventual presence of different climatic conditions if there is time-averaging occurring in the shell bed. It is the case here, with specimens UD53435 and C36472 showing higher (colder) $\delta^{18}O$ ratios compared to specimen C36478. We suggest that even if the different species do not have exactly the same number of samples per season, this resolution effect does not alter significantly the interpretation of the assemblage, because of the absence of significant growth lines during thermal peaks in summer and winter.

The Ramsholt Member is up to 7.5m thick (Balson, *et al*, 1993) and was deposited during a wide interval of time (4.4 – 3.8 Ma, De Schepper *et al*., 2009), with little indication of the rate of deposition. From these considerations came the idea to unlock this problem of warm- and cold-living species with a finer stratigraphic approach.

*Focus on Shell Bed II*

The results of the $\delta^{18}O$ analysis (using the same value of + 0.10 ‰ for the $\delta^{18}O_{sw}$ signature) of the shells from shell bed II (SBII) provided the same picture as the Ramsholt Member as a whole (cf. above), with *A. islandica* giving colder conditions, both in winter (≈ 6 $^{0}$C) and in summer (≈ 12 $^{0}$C), *A. opercularis* giving a wide seasonal range with cold winter and warm summer, and *G. obovata* and *C. squamulosa ampla* giving warmer conditions, both in winter (about 10 $^{0}$C) and in summer (> 14 $^{0}$C). From this perspective, two hypotheses emerge to interpret the SB II assemblage (and more broadly the Ramsholt Member assemblage):

-These specimens lived at the same time, but in different environments (at different depths for example) and were mixed by current transport, even if we have no example of a similar assemblage in modern ecosystems.

- Or the different specimens lived in different temperature conditions (i.e., during different time intervals), with sedimentation rates slow enough so the different periods cannot be distinguished.

Neither of these hypotheses can be irrevocably excluded, but the following section will detail why we consider the second hypothesis is more likely.

*Did these four species live contemporaneously in the same environment?*

As seen above, growth lines do not suggest that each recorded a specific period of the year and all four species provided at least several years with smooth variations of $\delta^{18}O$, which is a good indicator of continuous growth and thus record of the actual environmental conditions (Goodwin, *et al*, 2003). Differences in depth could explain differences in reconstructed summer temperatures in strongly stratified environments, but in this case winter temperatures should be relatively close. In our data set, reconstructed temperatures from $\delta^{18}O$ analysis show a clear shift in winter temperature: *C. squamulosa ampla* winter temperatures are roughly equivalent to *A. islandica* summer temperatures (in the 10–12 $^{0}$C range), and *A. islandica* winter temperatures are about 6 $^{0}$C colder compared to *C. squamulosa ampla* winters.

A counterargument to the temporal mixing is the lack of traces of reworking or storm events, the good preservation of shells (especially the fragile outer layer of the carditids), and the presence of articulated specimens, which are supposed to be particularly fragile due to the quick degradation of the ligament. However, it is now well documented that time-averaging commonly occurs in marine shelf assemblages, which can be a mixture of shells that lived over thousands or tens of thousands of years (Kidwell, 1997, 2013), even in the absence of differential degradation of shells in the case of long-term accumulation.

*The Coralline Crag's temperature regimes*

Based on their seasonal range and winter temperature, two climatic settings are identified (Fig. 11). A warm setting, with mean summer temperatures in the 14–15 $^{0}$C range and mean winter

temperatures in the 10–12 $^{0}$C range, includes all the *C. squamulosa ampla* and *G. obovata* shells, plus one *A. opercularis* (C36478). Reconstructed winter SST is similar among all the three species, and a continuous, highly resolved record of winter conditions in specimen C36478 confirms the accuracy of the reconstruction. Summer temperatures are homogenous among *C. squamulosa ampla* and *G. obovata* specimens, but the *A. opercularis* shell shows much warmer conditions, above 20 $^{0}$C, which is the temperature associated with warm-temperate conditions. The lower summer values for *C. squamulosa ampla* and *G. obovata* could be explained by the presence of a thermocline in summer, but this would require that the different species would have been mixed by current transport. The winter temperature values of this warmer setting correspond to previously described warm-temperate conditions (>10 °C for winter) and are commonly accepted for the Coralline Crag's climate, on the basis of dinoflagellates (Head, 1997), planktonic foraminifera (Jenkins & Houghton, 1987), ostracods (Wood *et al*., 1993) and bivalves (Strauch, 1968). These studies also provided warmer summer temperatures compared to *C. squamulosa ampla* and *G. obovata* which once again could be explained by the presence of stratified waters (as some of these studies focus on organisms living at the surface). Warmer conditions have also been described, notably from the presence of the bryozoan *Metrarabdotos*, now confined to the Caribbean, where the seafloor temperature never gets cooler than 16 $^{0}$C (Cheetham, 1967; Taylor & Taylor, 2012). One can also remark that the warm temperatures from the shell C 36478 are well above modern southern North-Sea summer temperatures (16–17 $^{0}$C). Finally, warm summer temperatures (> 15 $^{0}$C) have also been described from the isotopic signatures of the brachiopod *Pliothyrina maxima* Charlesworth 1837 from Sudbourne Park (Vignols *et al.*, 2019).

Another method to approach the depth at which the specimens lived, and thus their position relatively to the summer thermocline would be to look at the correlation between $\delta^{18}$O and $\delta^{13}$C profiles. Above the thermocline, high respiration rates (releasing light carbon isotopes) coupled with high temperatures on the seafloor (light oxygen isotopes) would result in covariation of both profiles (Arthur *et al*, 1983; Krantz, 1990). However, our results shows that even if this covariation occurs for the *A. opercularis* profiles, we also observe anti-phase variation for most of the *A. islandica* specimens, and unclear or absence of correlation for the two other species. As noted by Johnson *et al*. (2017), there are exceptions to this general pattern, and "patterns of $\delta^{13}$C variation in relation to $\delta^{18}$O are not an infallible guide to hydrographic setting".

A temperature of 16 $^{0}$C is also considered as the upper limit of the thermal tolerance of *A. islandica*, in the North Sea at least (Witbaard & Bergman, 2003). Along with one specimen of

*A. opercularis*, the five shells from this species manifest the cold setting observed in our data, with winter temperatures in the 6–7 $^{0}$C range and summer in the 11–12 $^{0}$C range, which has not been extensively described (see Vignols *et al*. (2019): "irrespective of their statistical significance, there are only small differences between the values from the 'cool' and 'warm' species for all taxon mean temperature from ontogenic data […] we can only infer small fluctuations in marine climate from these data"), even if this idea is already mentioned in Johnson *et al.*, (2009). However, 5 $^{0}$C shifts in mid-latitude North Atlantic shallow marine and terrestrial environments have been documented elsewhere for the Pliocene (De Schepper *et al.*, 2013; Bachem *et al*, 2016; Dearing Crampton-Flood *et al.*, 2018).

These climatic oscillations, with a 4 $^{0}$C shift in winter temperature (and about 2–3 $^{0}$C for summers), would have needed to be long enough to allow the settlement of long-lived species like *A. islandica*, and the replacement of the Lusitanian faunas by a boreal one (and *vice versa*). This is why we suggest that these oscillations would have been of glacial/interglacial type.

Considering these elements and under the assumption that the $\delta^{18}O_{sw}$ we used is reasonable we suggest that the thermal tolerance of the different species remained stable through time. This assertion is also supported by the timing of the growth line formation and the range of reconstructed temperatures (still with a $\delta^{18}O_{sw}$ of + 0.1‰) for *A. islandica*, which are like modern specimens (Schöne *et al.*, 2005; Witbaard, 1999). Also, it is not only the few considered species of boreal and Lusitanian affinities that are mixed, but complete faunas from a wide array of phyla (see Introduction, and Long & Zalasiewicz (2011) for molluscs), making the hypothesis of thermal niche change unlikely. However, if we consider that the thermal tolerances of the species remain stable through time, *A. islandica* and *Centrocardita* spp. are supposed to live in different biogeographic regions, as they cannot be found alive together anywhere on the European Atlantic coasts. Based on these elements we suggest that *A. islandica* and *C. squamulosa ampla* did not live at the same time, but at different periods, under two distinct climatic settings.

## Conclusion

In this study, we used geochemical proxies ($\delta^{13}C$ and $\delta^{18}O$) to understand the marine climatic conditions under which the Ramsholt Member of the Coralline Crag Formation (Suffolk, United Kingdom) was produced during the Early Pliocene. Our results show that this member was produced under two different climatic conditions on the seafloor, maybe of glacial/interglacial type. Assuming a $\delta^{18}O_{sw}$ of +0.1 ‰, we describe a warm-temperate setting, represented by *C. squamulosa ampla*, *G. obovata* and some *A. opercularis*, which shows winter temperatures in the 10 $^{0}$C range and summer temperatures above 14 $^{0}$C. The cold-temperate setting is represented by the *A. islandica* shells and some *A. opercularis*. Winter temperatures for this cold-setting are about 6–7 $^{0}$C while summer temperatures are in the 12 $^{0}$C range. The range of reconstructed temperatures and the timing of growth line formation also suggest that the thermal niche and phenology of the different species was not radically different from modern analogues. The mixing of shells from these two different settings in single shell beds also highlights the time-averaging that occurred at certain horizons in this member, making geochemical analysis essential to understand the fossil assemblages: as we have no examples of a modern seafloor ecosystem hosting both *A. islandica* and *C.* spp., ecological uniformitarianism alone is insufficient here to reconstruct Ramsholt Member environments.



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Table 1:

| **Shell ID** | **Species** | **Origin** | **Horizon** | **Articulated** |
|---|---|---|---|---|
| UD53411 | *Centrocardita s. ampla* | Field collection (A. L. A. Johnson) | Shell Bed II | No |
| UD53412 | *Centrocardita s. ampla* | Field collection (A. L. A. Johnson) | Unknown | No |
| UD53429 | *Centrocardita s. ampla* | Field collection (A. L. A. Johnson) | Unknown | No |
| IPSMG:EF.2022.2333.1 | *Centrocardita s. ampla* | Ipswich Museum | Unknown | No |
| IPSMG:EF.2022.2333.2 | *Centrocardita s. ampla* | Ipswich Museum | Unknown | No |
| UD53430 | *Glycymeris obovata* | Field collection (A. L. A. Johnson) | Shell Bed II | No |
| C36252 (01) | *Glycymeris obovata* | Sedgwick Museum | Unknown | Yes |
| C36256 (02) | *Glycymeris obovata* | Sedgwick Museum | Unknown | Yes |
| UD53431 | *Arctica islandica* | Field collection (A. L. A. Johnson) | Unknown | Yes |
| UD53432 | *Arctica islandica* | Field collection (A. L. A. Johnson) | Unknown | No |
| UD53433 | *Arctica islandica* | Field collection (A. L. A. Johnson) | Unknown | No |
| IPSMG:EF.2022.2333.3 | *Arctica islandica* | Ipswich Museum | Unknown | Yes |
| UD53434 | *Arctica islandica* | Field collection (J.F. Cudennec) | Shell Bed II | No |
| UD53435 | *Aequipecten opercularis* | Field collection (A. L. A. Johnson) | Shell Bed II | Yes |
| C36472 | *Aequipecten opercularis* | Sedgwick Museum | Unknown | Yes |
| C36478 | *Aequipecten opercularis* | Sedgwick Museum | Unknown | Yes |

Table 2:

| Species | | Winter | Median | Summer | Range |
|---|---|---|---|---|---|
| ***C. squamulosa ampla*** | $\delta^{18}O$ | 2.63 ‰ | 1.82 ‰ | 0.95 ‰ | 1.68 ‰ |
| | T $^{0}C$ | 8.45 $^{0}C$ | 11.97 $^{0}C$ | 15.73 $^{0}C$ | 7.28 $^{0}C$ |
| ***G. obovata*** | $\delta^{18}O$ | 2.66 ‰ | 1.77 ‰ | 0.97 ‰ | 1.69 ‰ |
| | T $^{0}C$ | 8.34 $^{0}C$ | 12.17 $^{0}C$ | 15.67 $^{0}C$ | 7.33 $^{0}C$ |
| ***A. islandica*** | $\delta^{18}O$ | 3.21 ‰ | 2.43 ‰ | 1.51 ‰ | 1.70 ‰ |
| | T $^{0}C$ | 5.93 $^{0}C$ | 9.32 $^{0}C$ | 13.31 $^{0}C$ | 7.38 $^{0}C$ |
| ***A. opercularis*** | $\delta^{18}O$ | 2.14 ‰ | 1.19 ‰ | -0.93 ‰ | 3.07 ‰ |
| | T $^{0}C$ | 7.30 $^{0}C$ | 11.13 $^{0}C$ | 20.29 $^{0}C$ | 12.99 $^{0}C$ |

Table 3:

| **Shell ID** | **Number of samples** | **Number of seasons** | |
|---|---|---|---|
| | | **Winter** | **Summer** |
| UD53411 | 30 | 2 | 3 |
| UD53412 | 30 | 3 | 2 |
| UD53429 | 33 | 6 | 6 |
| IPSMG:EF.2022.2333.1 | 24 | 4 | 4 |
| IPSMG:EF.2022.2333.2 | 24 | 5 | 5 |
| **Average *Centrocardita*** | **28.2** | **4** | **4** |
| **Total *Centrocardita*** | **141** | **20** | **20** |
| UD53430 | 44 | 5 | 6 |
| C36252 (01) | 40 | 6 | 5 |
| C36256 (02) | 30 | 4 | 3 |
| **Average *Glycymeris*** | **38** | **3.75** | **3.5** |
| **Total *Glycymeris*** | **114** | **15** | **14** |
| UD53431 | 40 | 3 | 3 |
| UD53432 | 45 | 1 | 1 |
| UD53433 | 45 | 3 | 4 |
| IPSMG:EF.2022.2333.3 | 59 | 5 | 5 |
| UD53434 | 60 | 6 | 6 |
| **Average *Arctica*** | **49.8** | **3.6** | **3.8** |
| **Total *Arctica*** | **249** | **18** | **19** |
| UD53435 | 26 | 2 | 1 |
| C36472 | 28 | 4 | 3 |
| C36478 | 28 | 1 | 1 |
| **Average *Aequipecten*** | **27.3** | **2.3** | **1.7** |
| **Total *Aequipecten*** | **82** | **7** | **5** |

Figure 1:

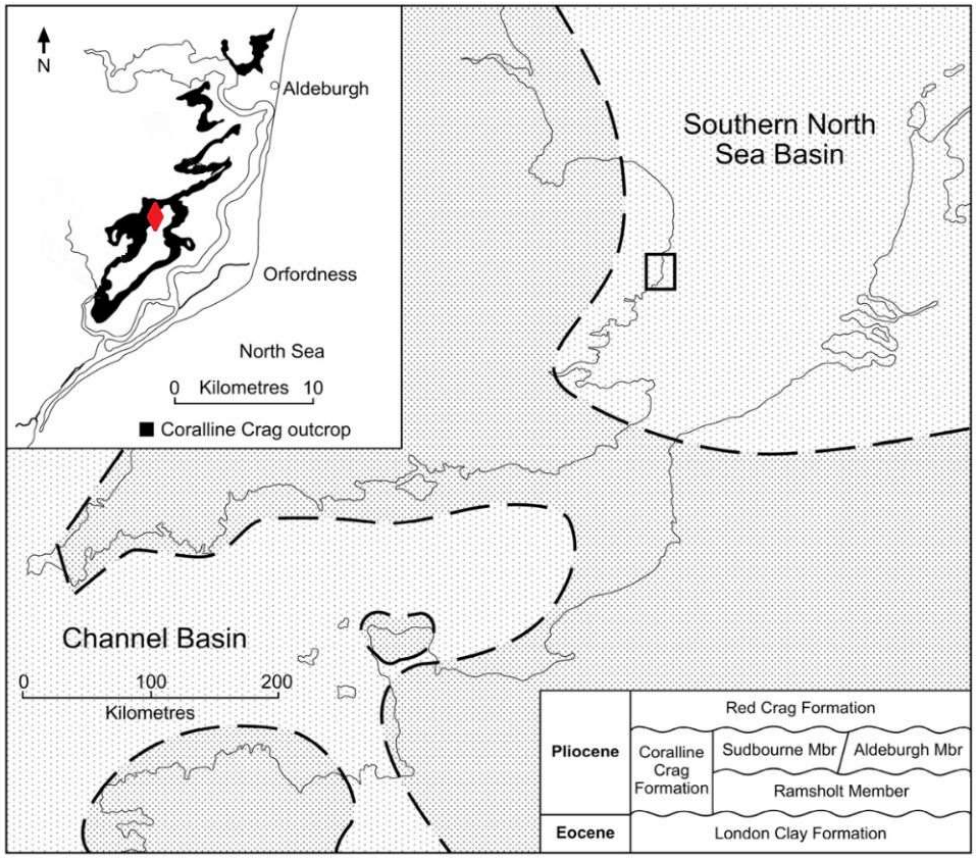


Figure 2:

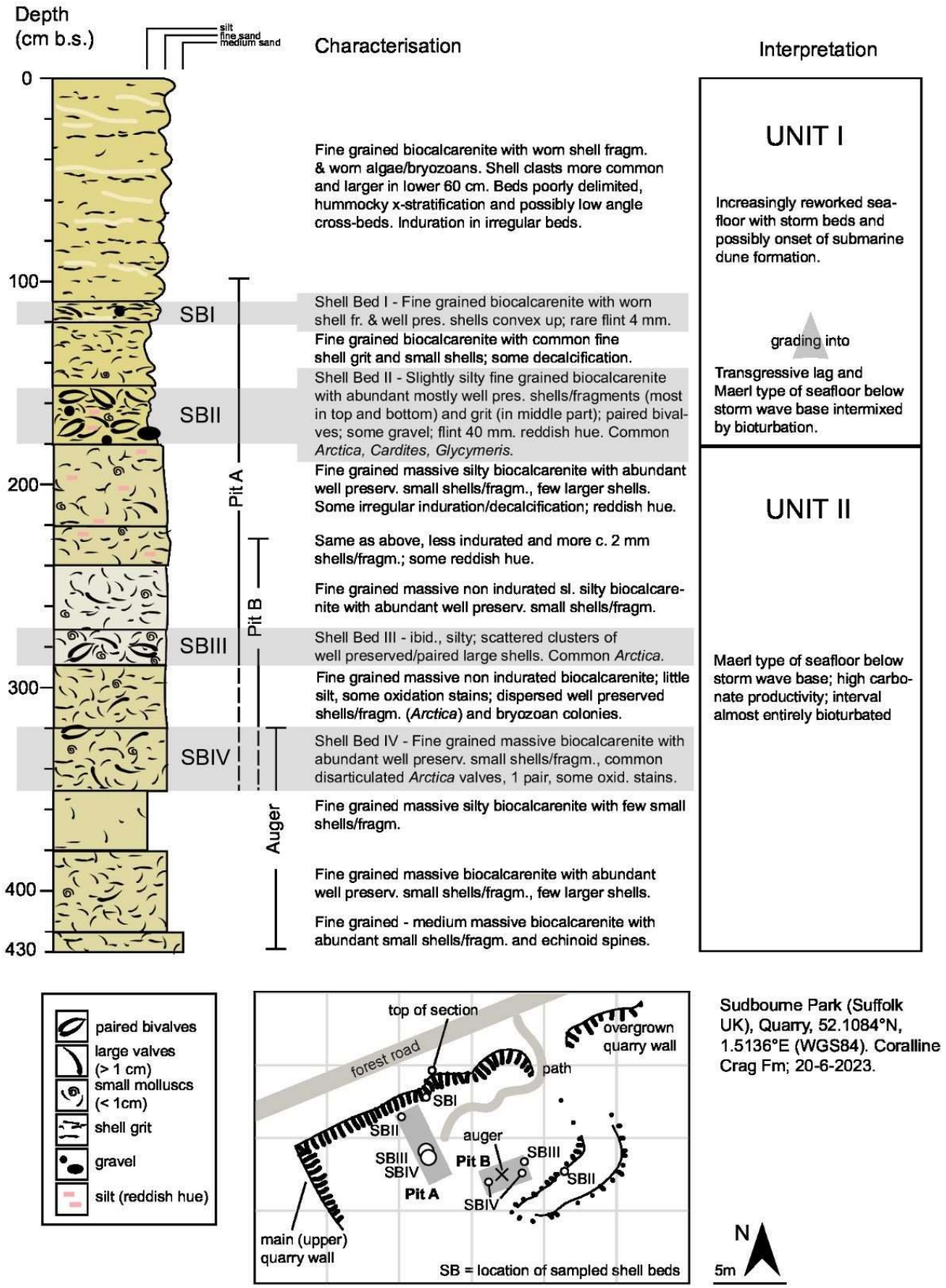

Depth
(cm b.s.)
silt
fine sand
medium sand
Characterisation
Interpretation
0
100
200
300
400
430
SBI
SBII
SBIII
SBIV
Pit A
Pit B
Auger
Fine grained biocalcarenite with worn shell fragm. & worn algae/bryozoans. Shell clasts more common and larger in lower 60 cm. Beds poorly delimited, hummocky x-stratification and possibly low angle cross-beds. Induration in irregular beds.
Shell Bed I - Fine grained biocalcarenite with worn shell fr. & well pres. shells convex up; rare flint 4 mm.
Fine grained biocalcarenite with common fine shell grit and small shells; some decalcification.
Shell Bed II - Slightly silty fine grained biocalcarenite with abundant mostly well pres. shells/fragments (most in top and bottom) and grit (in middle part); paired bivalves; some gravel; flint 40 mm. reddish hue. Common Arctica, Cardites, Glycymeris.
Fine grained massive silty biocalcarenite with abundant well preserv. small shells/fragm., few larger shells. Some irregular induration/decalcification; reddish hue.
Same as above, less indurated and more c. 2 mm shells/fragm.; some reddish hue.
Fine grained massive non indurated sl. silty biocalcarenite with abundant well preserv. small shells/fragm.
Shell Bed III - ibid., silty; scattered clusters of well preserved/paired large shells. Common Arctica.
Fine grained massive non indurated biocalcarenite; little silt, some oxidation stains; dispersed well preserved shells/fragm. (Arctica) and bryozoan colonies.
Shell Bed IV - Fine grained massive biocalcarenite with abundant well preserv. small shells/fragm., common disarticulated Arctica valves, 1 pair, some oxid. stains.
Fine grained massive silty biocalcarenite with few small shells/fragm.
Fine grained massive biocalcarenite with abundant well preserv. small shells/fragm., few larger shells.
Fine grained - medium massive biocalcarenite with abundant small shells/fragm. and echinoid spines.
UNIT I
Increasingly reworked seafloor with storm beds and possibly onset of submarine dune formation.
grading into
Transgressive lag and Maerl type of seafloor below storm wave base intermixed by bioturbation.
UNIT II
Maerl type of seafloor below storm wave base; high carbonate productivity; interval almost entirely bioturbated
paired bivalves
large valves (> 1 cm)
small molluscs (< 1cm)
shell grit
gravel
silt (reddish hue)
top of section
forest road
overgrown quarry wall
path
SBI
SBII
auger
SBIII
SBIV
Pit B
Pit A
main (upper) quarry wall
SB = location of sampled shell beds
N
5m
Sudbourne Park (Suffolk UK), Quarry, 52.1084°N, 1.5136°E (WGS84). Coralline Crag Fm; 20-6-2023.

Figure 3:

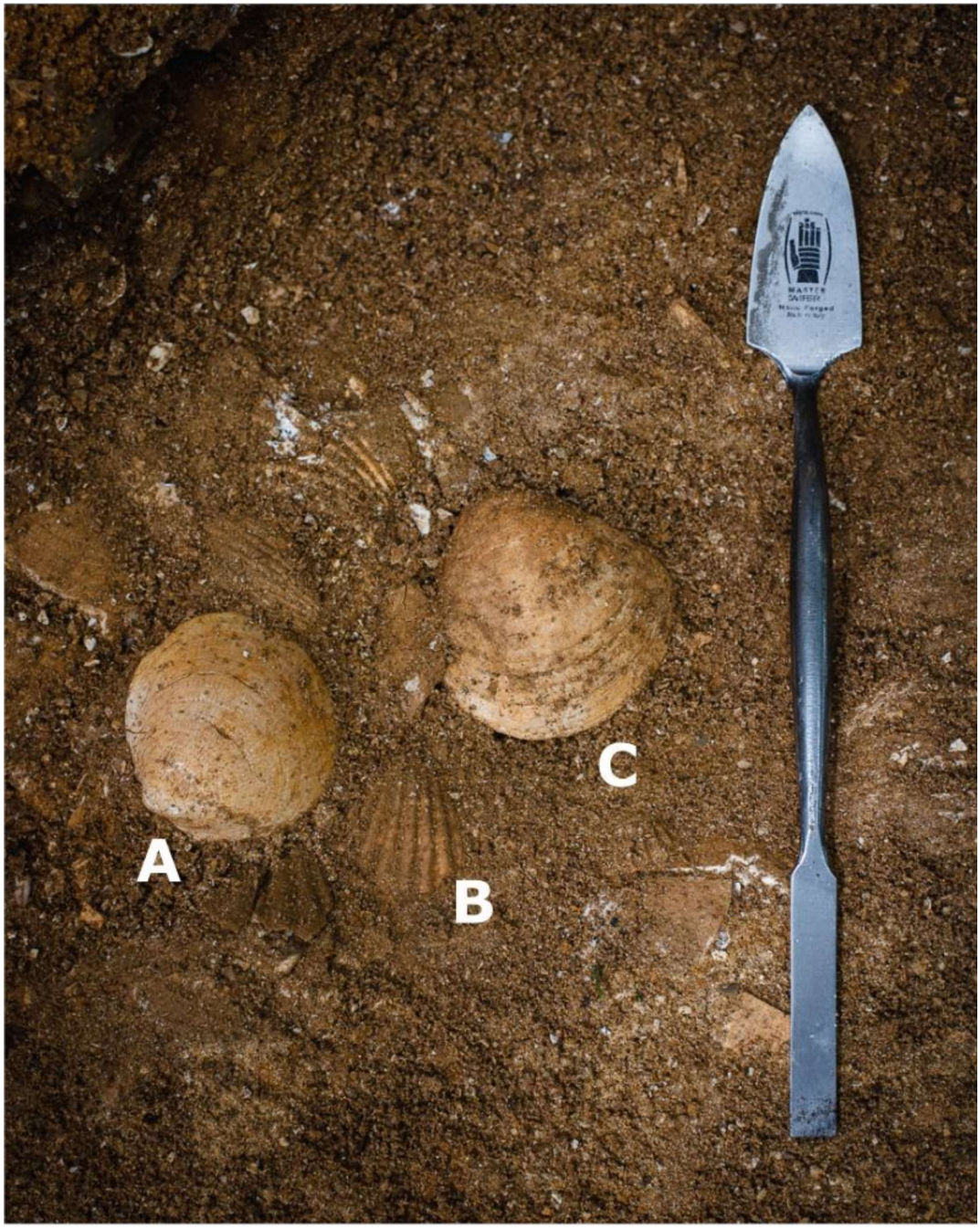
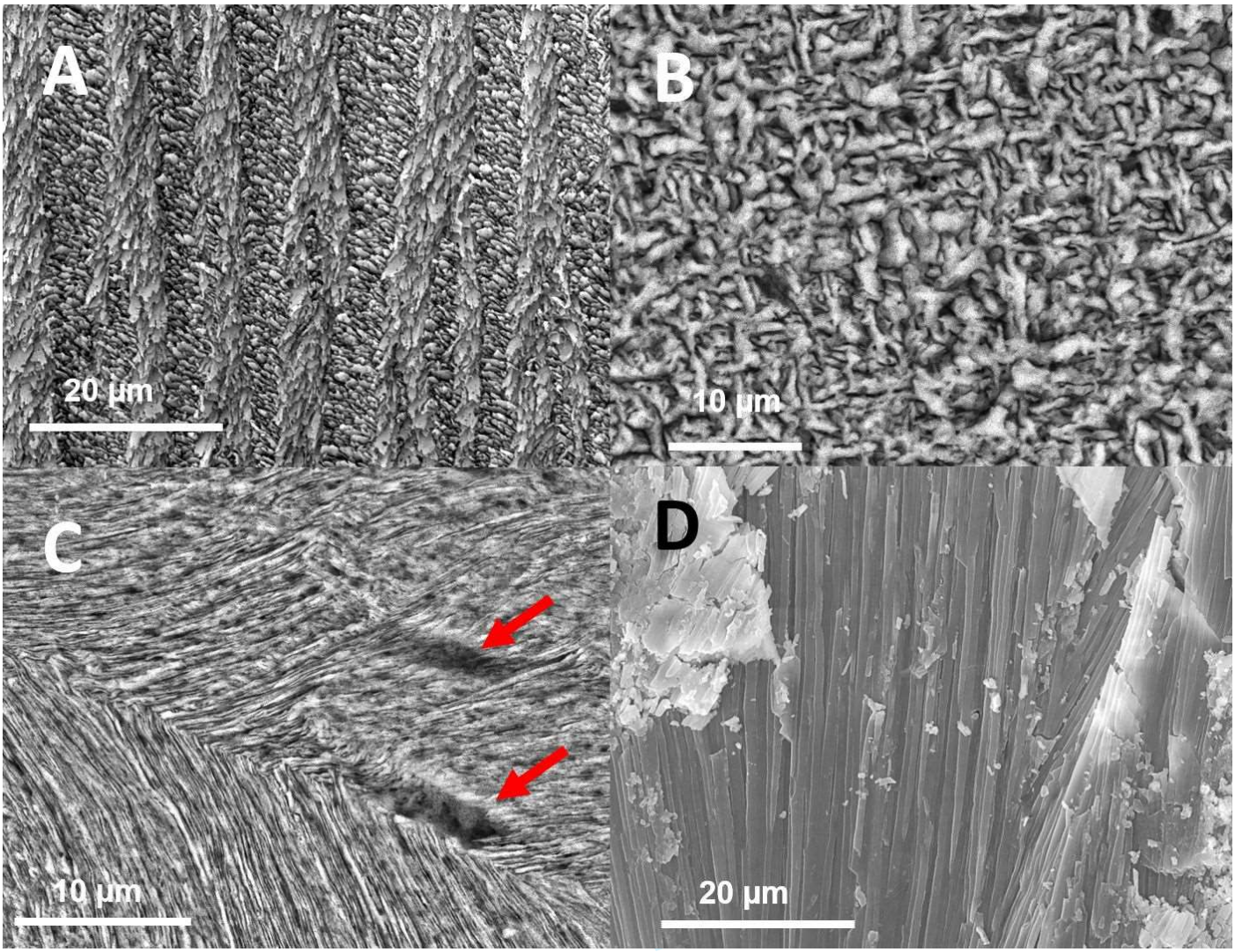


Figure 4:



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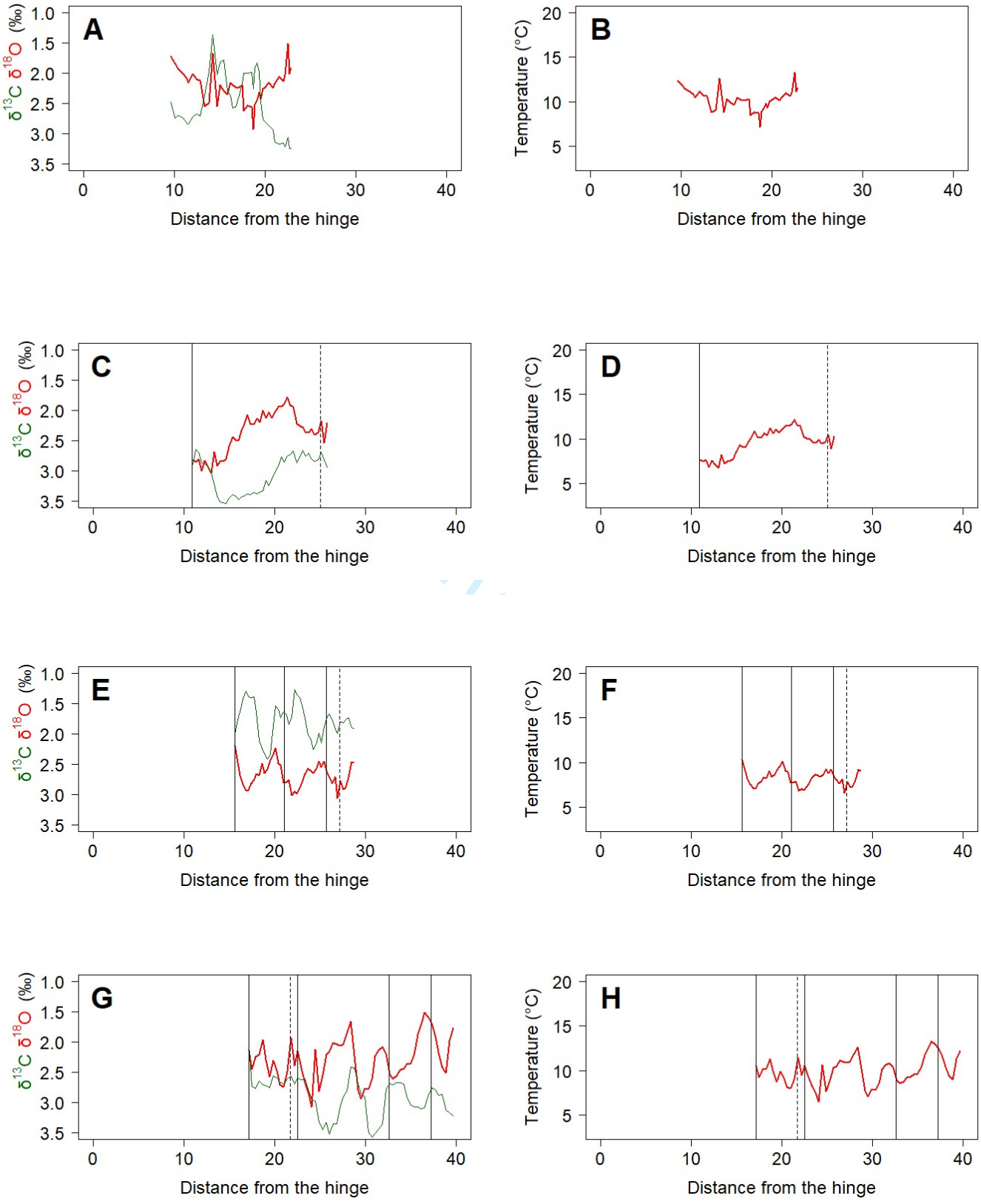

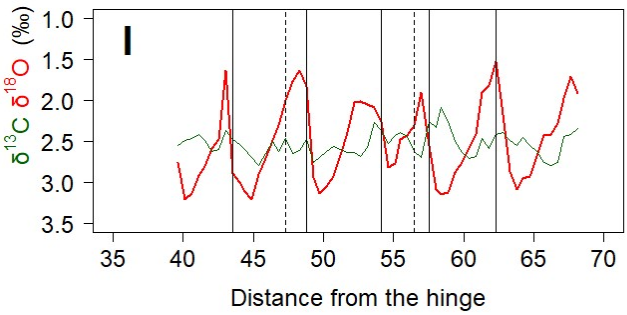


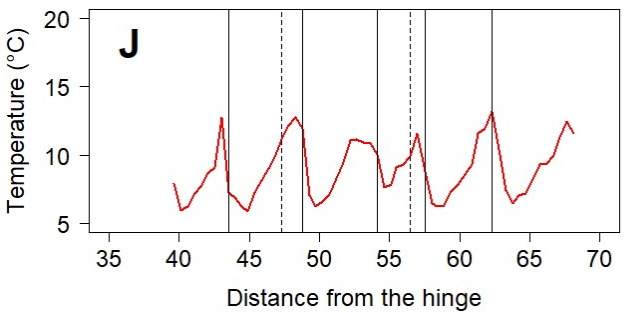

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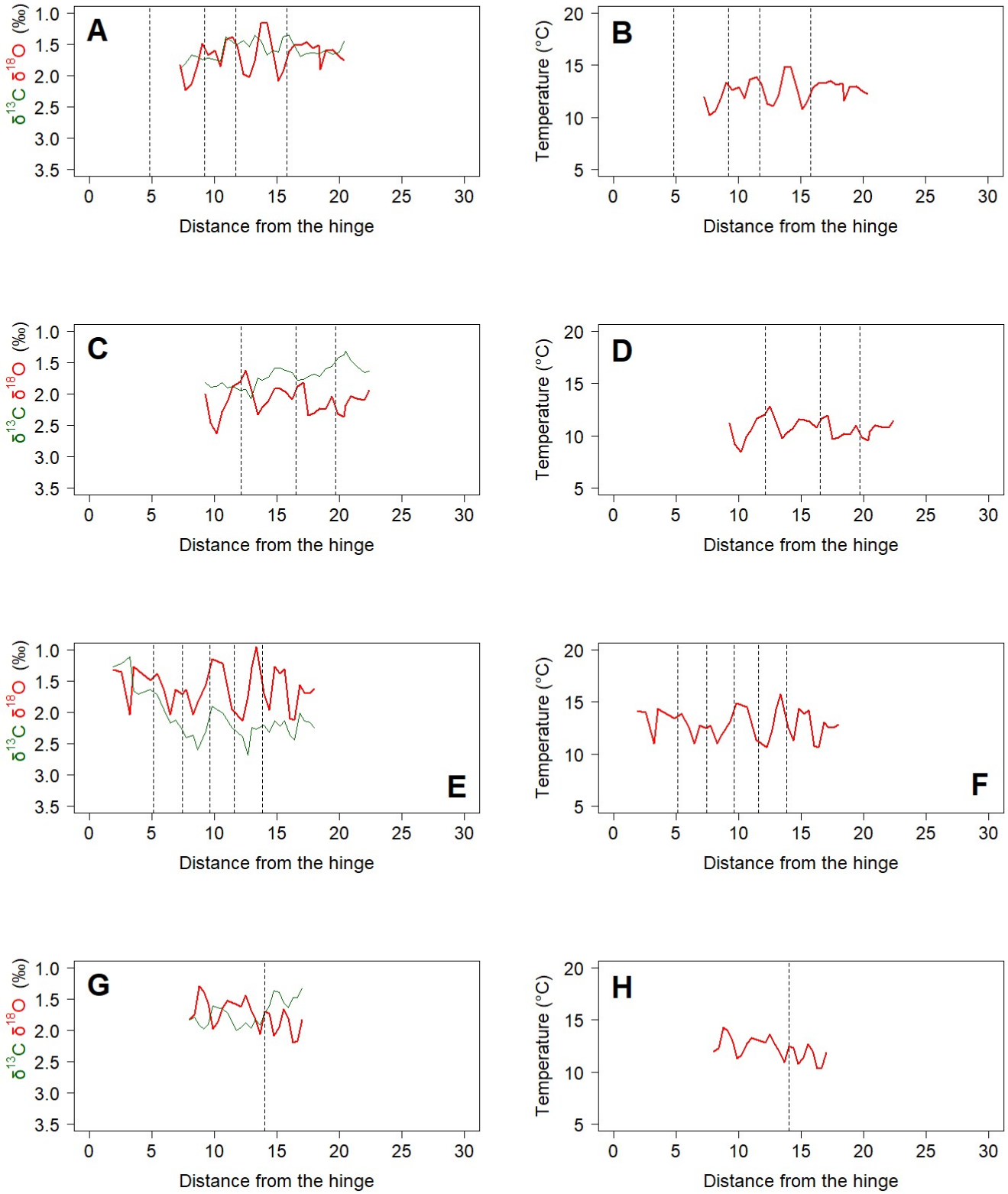

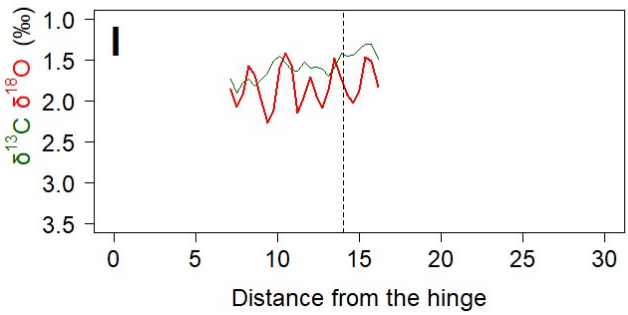


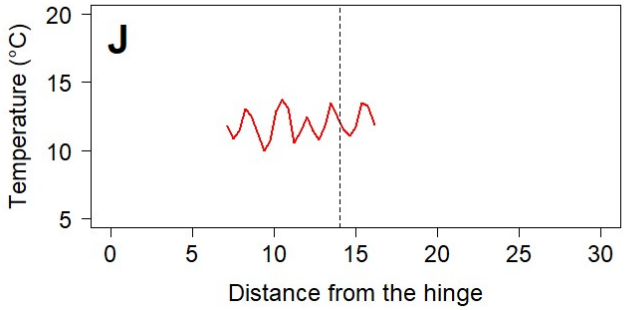

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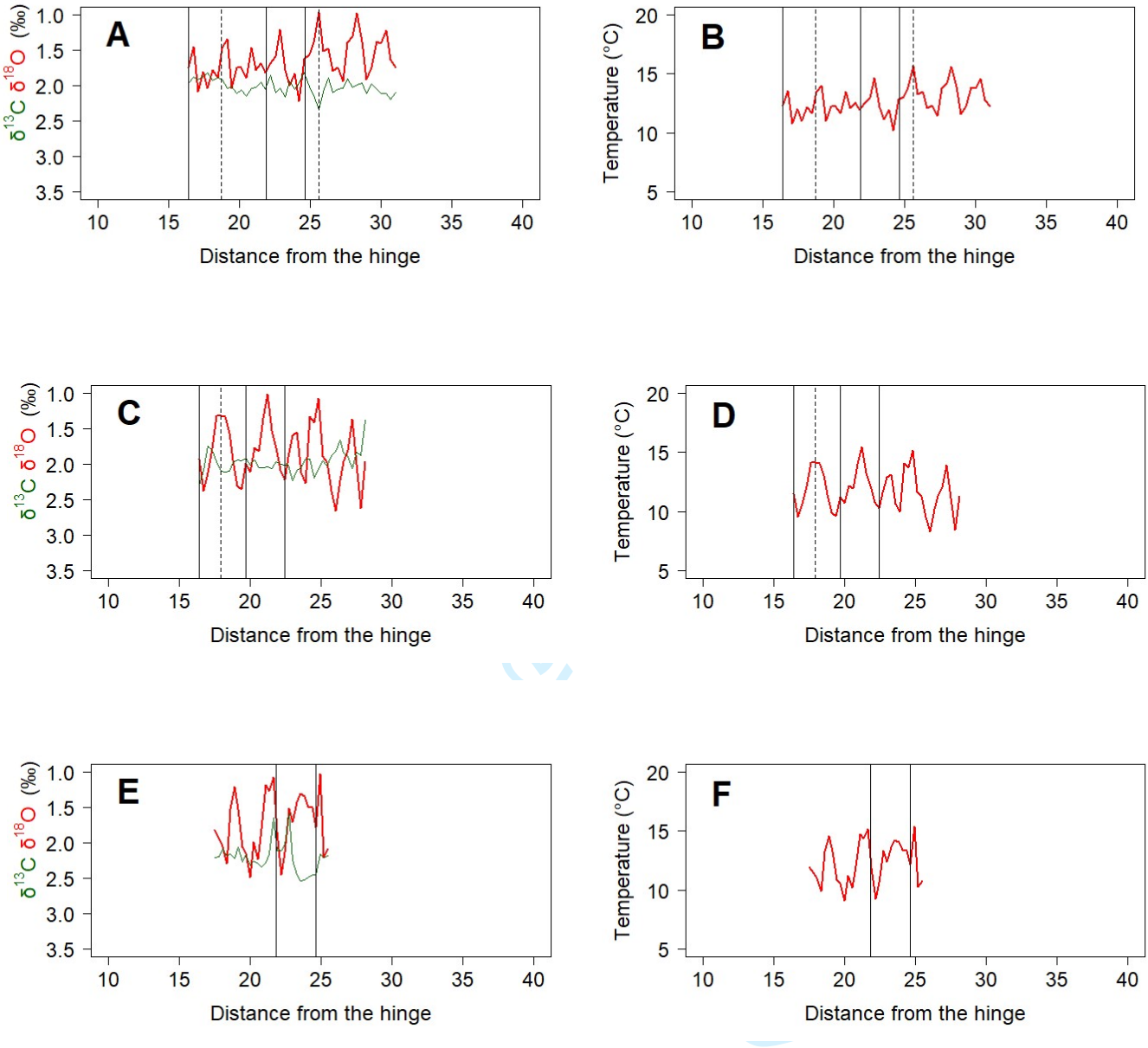

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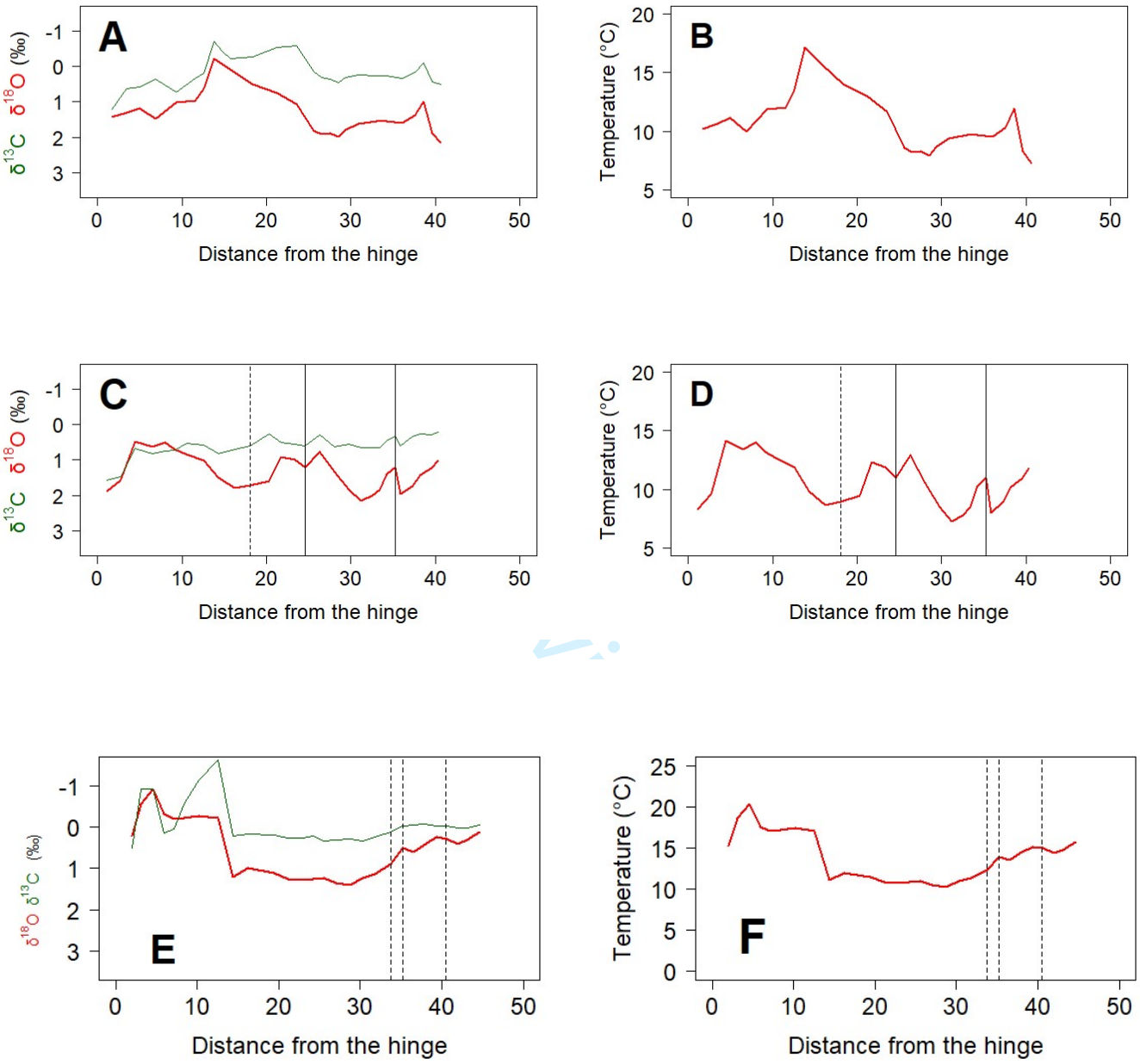

A
B
C
D
E
F
δ13C δ18O (‰)
δ18O δ13C (‰)
Temperature (°C)
Distance from the hinge

Figure 9:

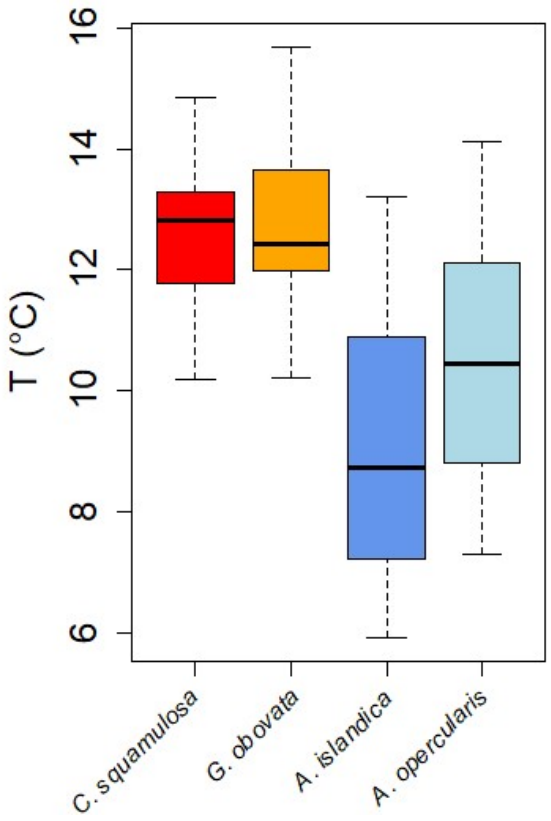
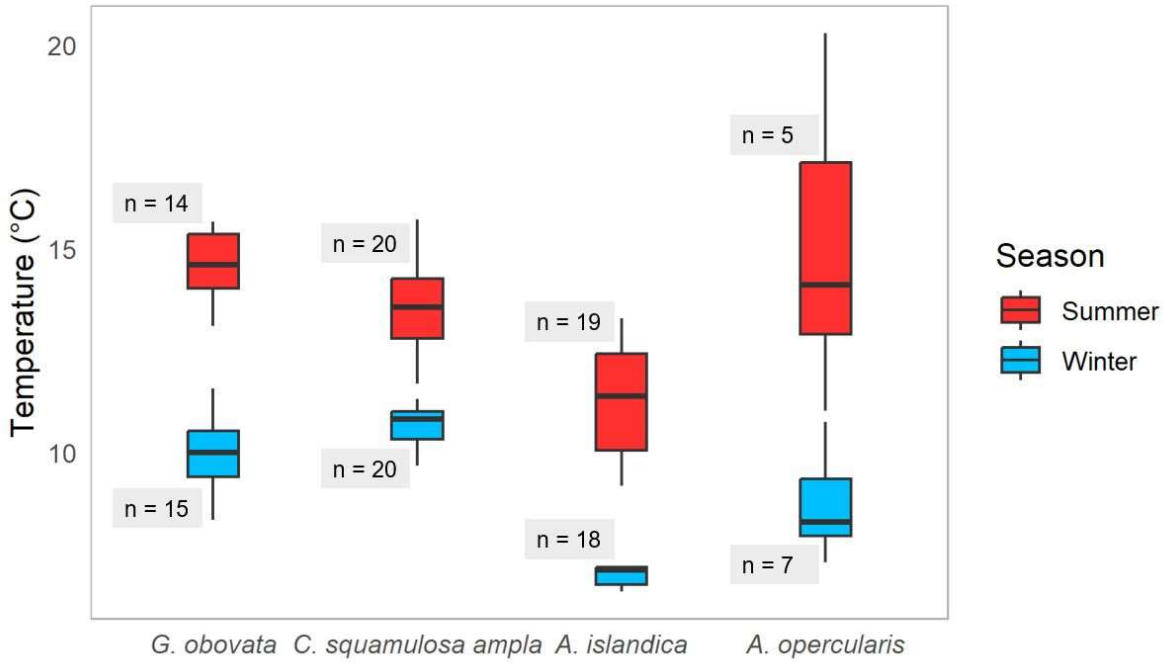


Figure 10:



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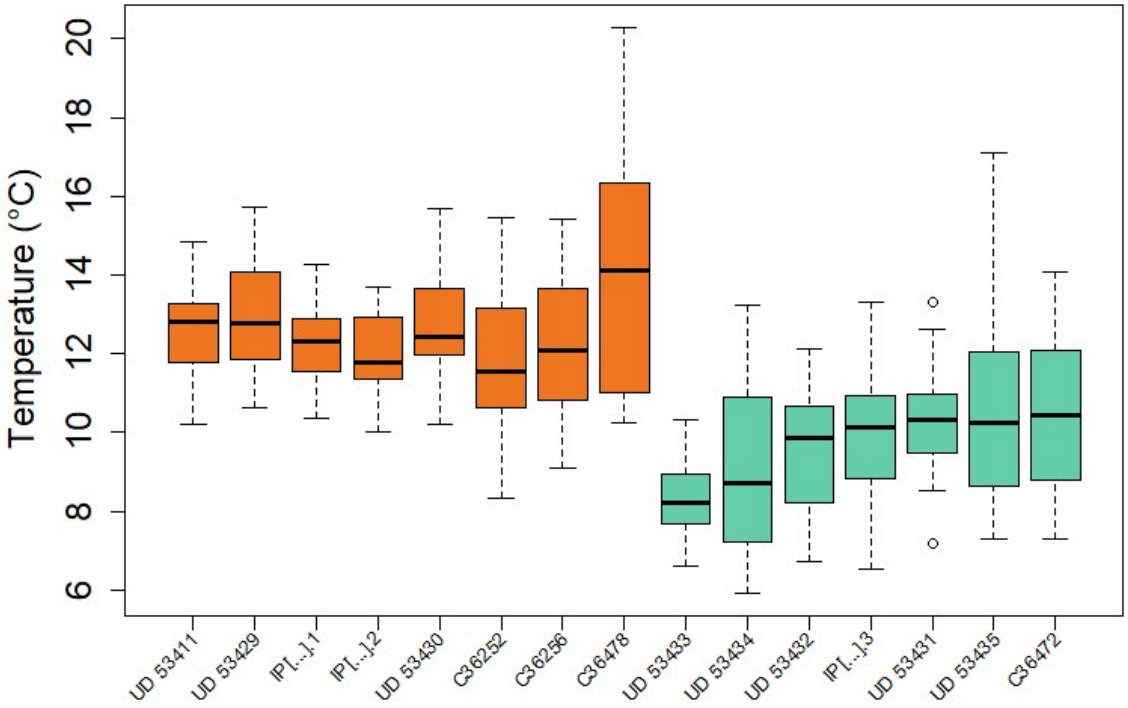

# Tables and Figure captions

**Table 1:** Details of the 16 analysed shells. Museum specimens come from previous collecting and could not be attributed to a specific shell bed. Based on the recorded height in the Sudbourne Park section, some of the specimens previously collected by the authors could be attributed to specific shell beds. UD: University of Derby, CXXXXX: Sedgwick Museum (University of Cambridge), IPSMG: Ipswich Museum of Natural History.

**Table 2:** Extreme $\delta^{18}O$ values and temperatures, together with the median value and range, from each of the four species. *A. islandica* shows the highest $\delta^{18}O$, while *A. opercularis* shows the lowest values (highest temperature) and the widest range. The three aragonitic species have a very similar $\delta^{18}O$ range, despite a shift to higher values for *A. islandica*. Temperatures values are based on a $\delta^{18}O_{sw}$ of +0.10 ‰.

**Table 3:** Number of samples per shell and number of seasons for each of the 16 analysed shells.

**Figure 1:** Paleogeography of the Channel and southern North Sea Basin during the Pliocene. Dark grey areas represent land and dashed lines represent paleo-coastlines. Upper box represents the main outcrops of the Coralline Crag formation (red diamond: Sudbourne Park) while lower box represents the chronology of the Suffolk crags. Modified from Johnson *et al.* (2009).

**Figure 2:** Sketch-map and stratigraphic log of the investigated site, showing the different shell beds (SB1–SBIV). All four shell beds contain the four investigated species, but SBII shows best preservation, and all four species in abundance. SBI is richer in *C. squamulosa* and *A. opercularis*, while SBIII and IV contained more *A. islandica*.

**Figure 3:** Context picture of SBII with adjacent, unbroken, convex-up valves of A) *G. obovata*, B) *C. squamulosa ampla* and C) *A. islandica*. The tool is approx. 20 cm long.

**Figure 4**: SEM micrographs of preserved shell ultrastructures of the four species investigated in this study. A: crossed-lamellar ultrastructure of the inner outer shell layer (iOSL) of *C. squamulosa ampla*. B: Crossed acicular ultrastructure of the iOSL of *A. islandica;* C: open tubules (red arrows) in the crossed-lamellar iOSL of *G. obovata*; D: Internal foliated shell ultrastructure from the auricles of *A. opercularis*.

**Figure 5**: Isotopic profiles (left) and temperature reconstruction (right) data from *A. islandica* shells from Sudbourne Park. Isotopic values and reconstructed temperatures are plotted against

the distance from the origin of growth (hinge); measured in mm. Vertical lines represent noticeable growth interruptions. $\delta^{18}O$ data are in red and $\delta^{13}C$ are in green. Temperature reconstructions are based on a modelled $\delta^{18}O_{sw}$ value of +0.1 ‰. A–B: UD53431; C–D: UD 53432; E–F: UD53433 ; G–H: IPSMG:EF.2022.2333.3; I–J: UD53434.

**Figure 6:** Isotopic profiles (left) and temperature reconstruction (right) data from *C. squamulosa ampla* shells from Sudbourne Park. Isotopic values and reconstructed temperatures are plotted against the distance from the origin of growth (hinge); measured in mm. Vertical lines represent noticeable growth interruptions. $\delta^{18}O$ data are in red and $\delta^{13}C$ are in green. Temperature reconstructions are based on a modelled $\delta^{18}O_{sw}$ value of +0.1 ‰. A–B: UD53411; C–D: UD53412; E–F: UD53429 ; G–H: IPSMG:EF.2022.2333.1 ; I–J: IPSMG:EF.2022.2333.2.

**Figure 7:** Isotopic profiles (left) and temperature reconstruction (right) data from *G. obovata* shells from Sudbourne Park. Isotopic values and reconstructed temperatures are plotted against the distance from the origin of growth (hinge); measured in mm. Vertical lines represent noticeable growth interruptions. $\delta^{18}O$ data are in red and $\delta^{13}C$ are in green. Temperature reconstructions are based on a modelled $\delta^{18}O_{sw}$ value of +0.1 ‰. A–B: UD53430; C–D: C36252; E–F: C36256.

**Figure 8:** Isotopic profiles (left) and temperature reconstruction (right) data from *A. opercularis* shells from Sudbourne Park. Isotopic values and reconstructed temperatures are plotted against the distance from the origin of growth (hinge); measured in mm. Vertical lines represent noticeable growth interruptions. $\delta^{18}O$ data are in red and $\delta^{13}C$ are in green. Temperature reconstructions are based a modelled $\delta^{18}O_{sw}$ value of +0.1 ‰. A–B: UD53435; C–D: C 36472 ; E–F: C 36478.

**Figure 9:** Temperature boxplot of the four specimens from SBII. Horizontal black bars represent the median, and the boxes depict the interquartile range (IQR), where the lower and upper boundaries represent the first and third quartiles, respectively. Whiskers extend to the maximum and minimum temperature values.

**Figure 10:** Temperature boxplots of winter (blue) and summer (red) temperature for each of the four analysed species, based on all the summer/winter values of each specimen of each species. Horizontal black bars represent the median, and the boxes depict the interquartile range (IQR), where the lower and upper hinges represent the first and third quartiles, respectively. Whiskers extend to the maximum and minimum temperature values within 1.5 times the IQR

(two outliers were removed from a total of 118 data points). The reconstructed temperatures are based on a $\delta^{18}O_{sw}$ value of +0.1 ‰. The number of seasons used to calculate each boxplot is displayed in grey boxes.

**Figure 11:** Temperature boxplot of the specimens from the Ramsholt Member at Sudbourne Park. Horizontal black bars represent the median, and the boxes depict the interquartile range (IQR), where the lower and upper hinges represent the first and third quartiles, respectively. Whiskers extend to the maximum and minimum temperature values. Two climatic modes can be separated: a warm setting in orange, including all the *C. squamulosa ampla* and *G. obovata* shells, plus one *A. opercularis*, and a cold setting in green, including all the *A. islandica* and two *A. opercularis*.